# Influence of fire on native nitrogen-fixing plants and soil nitrogen status in ponderosa pine – Douglas-fir forests in western Montana

**J.A. Newland and T.H. DeLuca**

**Abstract**: Nitrogen fixing plants have been reported to play an important role in replacing N lost from soil in fire dominated ecosystems. Exclusion of fire from ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) – Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests of western Montana has lead to widespread changes in forest structure, composition, and function including a potential reduction in the occurrence of N-fixing plant species. We investigated the effect of fire exclusion and reintroduction of fire on the frequency, occurrence, and function of native N-fixing plant species at 11 paired burned and unburned sites in western Montana. These pairs had been either undisturbed since the early 1900s or had been repeatedly opened by logging and (or) fire over the last 80–100 years. Although the percent cover of N-fixing plants was low at all sites, the cover and frequency of N-fixing plants were significantly greater in sites exposed to fire than in the unburned sites and greater in repeatedly opened sites than in undisturbed sites. In contrast, levels of available N were significantly lower in burned sites compared with unburned sites and in repeatedly opened sites. Nitrogen-fixing plants may have played an important role in maintaining productivity in frequently burned ponderosa pine forests but now appear to be suppressed in fire-excluded forests.

**Résumé** : On rapporte que les plantes fixatrices d'azote jouent un rôle important dans le remplacement de l'azote qui est perdu dans les sols des écosystèmes dominés par le feu. L'exclusion du feu dans les forêts de pin ponderosa (*Pinus ponderosa* Dougl. ex Laws.) et de Douglas (*Pseudotsuga menziesii* (Mirb.) Franco) de l'ouest du Montana a entraîné d'importants changements dans la structure, la composition et la fonction de la forêt, incluant une réduction potentielle de l'occurrence des espèces végétales fixatrices d'azote. Nous avons étudié l'effet de l'exclusion et de la réintroduction du feu sur la fréquence, l'occurrence et la fonction des espèces de plantes indigènes fixatrices d'azote dans 11 sites pairés, brûlés ou non brûlés, situés dans l'ouest du Montana. Ces paires ont été soit non perturbées depuis le début des années 1900 soit ouvertes à plusieurs reprises par des opérations de récolte et (ou) des feux au cours des 80 à 100 dernières années. Même si le pourcentage de couverture des plantes fixatrices d'azote était faible dans tous les sites, la couverture et la fréquence des plantes fixatrices d'azote étaient significativement plus élevées dans les sites exposés au feu que dans les sites non brûlés et plus élevées dans les sites ouverts à plusieurs reprises que dans les sites non perturbés. Le niveau d'azote disponible, au contraire, était significativement plus faible dans les sites brûlés que dans les sites non brûlés ainsi que dans les sites ouverts fréquemment. Les plantes fixatrices d'azote pourraient avoir joué un rôle important dans le maintien de la productivité dans les forêts de pin ponderosa fréquemment affectées par le feu mais semblent maintenant supprimées dans les forêts protégées contre le feu.

[Traduit par la Rédaction]

## Introduction

Fire plays an important role in determining plant community composition and structure in ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) – Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in western Montana. Studies from this region place fire-frequency intervals at 13–50 years, which has maintained open stands of uneven-aged ponderosa pine (Arno 1976; Arno et al. 1995). Exclusion of high-frequency, low-intensity fires along with selective cutting of large ponderosa pines has led to the development of dense understory vegetation with many young Douglas-fir and to large accumulations of forest floor litter (Arno et al. 1995). These changes are also blamed for increased forest health problems; increased risk of high-intensity, stand-replacing wildfires; and decreased forest productivity (Harvey 1994; Arno 1996). How these changes affect understory shrubs and forbs has not been well documented (Fischer and Bradley 1987). Many early succession plants require disturbance to create open space, and in ponderosa pine – Douglas-fir forests of Montana, fire is the most common disturbance (Arno 1996).

Nitrogen is often considered to be limiting in forest ecosystems of the Inland Northwest, because low moisture availability and cool temperatures aid the accumulation of residues with high C/N ratios, which limits N mineralization (Kimmins 1996; Walley et al. 1996). Fire increases the recycling of N in forest litter and surface organic soil horizons resulting in a flush of inorganic N that can last for up to two growing seasons after the fire (Covington and Sackett 1992; DeLuca and Zouhar 2000). However, studies in the Inland Northwest have also shown that total N and mineralizable N

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may decrease after fire (Monleon et al. 1997; DeLuca and Zouhar 2000) resulting in a decrease in both the short- and long-term N availability in these forest soils.

Herbaceous N-fixing shrubs are common pioneer species following fire in prairie and forested ecosystems (Arianoutsou and Thanos 1996; Leach and Givnish 1996; Towne and Knapp 1996) and may play an important role in replacing N lost during fire (Hendricks and Boring 1999). A wide variety of N-fixing legumes and actinorhizal plants are common in western Montana forest ecosystems. These plants play an important role in forest community ecology by providing an important source of plant available N (Youngberg and Wollum 1976; Klemmedson 1979; Hendricks and Boring 1992; Trowbridge and Holl 1992). In addition to their role in the soil N cycle, some of these plants are also important species for wildlife browse and habitat (Noste and Bushey 1987).

Leach and Givnish (1996) found that N-fixing plant species diversity and abundance in prairie ecosystems have decreased in the absence of regular disturbance by fire. It is possible that changes in forest structure and composition in western Montana as a result of fire suppression (Arno et al. 1995) may be detrimental to N-fixing plants native to this region. The formation of a dense, closed canopy results in a light limited understory and an accumulation of organic N, both of which are inhibitory to N-fixing plants. It is likely that significant N accretion occurs in early successional stages (Jurgensen et al. 1991), but little work has examined understory vegetation in recently disturbed stands in these same forest types (Fischer and Bradley 1987; Jurgensen et al. 1991). Some N-fixing species have been studied in detail in the Inland Northwest, and in some cases, their N contributions to soils have been demonstrated (e.g., Conard et al. 1985). Species common to dry western Montana forests, like *Purshia tridentata* and *Ceanothus* spp., have been intensively studied, mostly because of their importance as wildlife browse and their perceived competition with tree regeneration (Gratkowski 1962) but not because of their significance as N fixers. The purpose of the work reported was to assess whether wildfire, prescribed fire, and fire exclusion have influenced the presence and abundance of native N-fixing plant species and whether this change is reflected in the soil N status.

## Materials and methods

### Site description

Six wildfire study sites were selected using a U.S. Forest Service data base listing all stands affected by wildfire in the last 3–10 years. Sites were selected on south- to west-facing slopes with a ponderosa pine or mixed ponderosa pine – Douglas-fir cover type and a Douglas-fir – ninebark (*Physocarpus malvaceus*) habitat type (Pfister et al. 1977) that had not otherwise been disturbed in at least 50 years. Six paired sites, each consisting of a site burned by wildfire and an unburned site with similar elevation, aspect, slope, and soil type, were selected from an initial list of over 30. Similar unburned control sites were only found where a road across a slope acted as a fire break or the fire was actively fought and a fire line separated burned from unburned areas. Four of the six sites are located in the Lolo National Forest (LNF) and two on the Bitterroot National Forest (BNF).

Five prescribed fire sites were selected based on time since treatment and previous harvest activity on these sites. Two sites were selected on the LNF and three at the Lick Creek Resource Demonstration Area in the BNF. Prescribed fires had been carried out in these sites in an orderly fashion with well-defined boundaries. Five prescribed burn sites were thus paired with five unburned control sites. The Lick Creek site is part of a larger research project investigating the use of prescribed fire in restoring presettlement conditions to seral ponderosa pine forests. Three units of the larger project were sampled for this study: two areas that had been selection harvested in 1992 and burned in the spring of 1993 and one that had been treated with a commercial thinning cut and a prescribed burn in the fall of 1993. All of the prescribed fire sites had been disturbed by harvest prior to fire treatment (Table 1).

The 11 study sites were selected to have similar habitat type and cover type, but other characteristics, such as slope, aspect, and elevation, varied among sites. Site characteristics are summarized in Table 1. Fire severity is a measure of the effect that fire has on the ecosystem and is a combination of the heat pulse into the air and down into the soil (Ryan and Noste 1985). Recent convention has focused on duff consumption as a measure of fire effects on soil and understory plant communities (Harrington 1999). Such information can be readily gathered at prescribed burn sites but is rarely available for wildfire-affected sites. Flame and scorch height can be used to estimate heat pulse from wildfires, but this may not provide any information regarding heat pulse into the soil. Fire severity is presented in Table 1 as a percentage of duff reduction for the prescribed fire sites and, for wildfire sites, simply classified as "low severity," "mixed severity," or "stand replacing."

Habitat types (Pfister et al. 1977) were determined; soil surface horizons were described; and other features, such as percent slope, aspect, and tree basal area, were measured at all sites. Soil color, texture, O horizon depth, and surface horizon depth were recorded from shallow soil pits dug in random locations for soil descriptions. Basal area was estimated using a prism and variable-radius plots, and in sites where salvage logging or thinning had occurred, prefire stand density was estimated from snags, downed trees, and (or) stumps.

### Sampling design

Four replicate plot centers were located in burned and unburned areas with similar soil properties and stocking levels. Once plot centers had been located in similar burned and unburned areas, fixed points were located at random distances between 0 and 15 m from the plot centers at compass settings of 45, 135, 225, and 315°. Native N-fixing shrubs were identified, and the percent ground cover for each shrub species present was estimated within 16-$m^2$ circles centered at each of these fixed subplot centers (Mueller-Dombois and Ellenberg 1974). Percent ground coverage for N-fixing forbs was estimated in four 1-$m^2$ squares located at the cardinal directions from the subplot center. Three sets of these plots were surveyed in each unburned and burned stand.

Nitrogen fixation potential for the plots was assessed by harvesting the aboveground biomass of each native N-fixing species in subplots where they were present. These plants were collected from inside the study subplot if possible or from adjacent areas if there was only a small amount of biomass. Non-N-fixing plants (one shrub and one forb for each site if both N-fixing shrubs and forbs were found) with the same life form and development stage and growing near N-fixing plants were selected (Weaver and Danso 1994; Bremer and van Kessel 1990; Shearer and Kohl 1986).

Percent cover of N-fixing species is reported as a proportion of the site. For example, a 1-$m^2$ square having 5% *Lupinus sericeus* is reported as having 0.05 *L. sericeus*. The numbers reported for each treatment at each site are means of 48 of the 1-$m^2$ squares, comprised of 16 squares in three sets of plots sampled in each treatment. The frequency of occurrence of N-fixing plants was determined by dividing the number of 1-$m^2$ squares at each subplot

**Table 1.** Selected site characteristics for all 11 study sites in western Montana.

| Site | Disturbance[a] | Elevation (m) | Aspect (degrees) | Slope (%) | Habitat type[b] | Soil subgroup | Fire type and severity[c] | Fire year |
|---|---|---|---|---|---|---|---|---|
| Frenchtown | H | 1100 | 170–180 | 10 | PsMe/SyAl | Mollic Eutoboralf | Underburn, 38% | 1995 |
| Cinderella Mountain | U | 1140 | 210–220 | 50–55 | PsMe/AgSp | Typic Xerochrept | SR wildfire | 1988 |
| Squaw Peak | U | 1310 | 190–220 | 30–35 | PsMe/PhMa | Dystic Eutrochrept | SR wildfire | 1994 |
| Alberton | U | 1450 | 180–190 | 40–45 | PsMe/CaGe | Typic Xerochrept | MS wildfire | 1988 |
| Henry Peak | U | 1410 | 240–250 | 55–60 | PsMe/PhMa | Typic Ustochrept | MS wildfire | 1994 |
| Echo Valley | H | 1140 | 270–280 | 15–20 | PsMe/SyAl | Typic Haploxeroll | Underburn, 36% | 1989 |
| Ward Mountain | U | 1610 | 90–100 | 25–30 | PsMe/PhMa | Dystic Cryochrept | SR wildfire | 1994 |
| Rock Creek | U | 1430 | 150 | 25–30 | PsMe/SyAl | Typic Ustochrept | MS wildfire | 1988 |
| Lick Creek 1 | H | 1410 | 180–190 | 20 | PsMe/SyAl | Typic Ustochrept | Underburn, 42% | 1993 |
| Lick Creek 2 | H | 1380 | 170–180 | 10 | PsMe/CaRu | Typic Ustochrept | Underburn, 42% | 1993 |
| Lick Creek 3 | H | 1400 | 160–180 | 20–25 | PsMe/CaRu | Typic Ustochrept | Underburn, 69% | 1993 |

[a]Harvest disturbance prior to fire: H, harvested within last 50 years; U, not harvested in last 50 years.
[b]PsMe, *Pseudostuga menzesii*; PhMa, *Physocarpus malvaceous*; SyAl, *Symphoricarpos albus*; CaRu, *Calamagrostis rubescens*; AgSp, *Agropyron spicatum*: CaGe, *Carex geryii* (for habitat type description, see Pfister et al. 1977).
[c]Fire severity for prescribed fire based on percent duff reduction and wildfires based on stand replacing (SR), mixed severity (MS), or low severity (LS).

that contained N-fixing plants by the number of 1-$m^2$ squares surveyed at each subplot.

Soil samples were collected from each of the four 1-$m^2$ forb-sampling areas in each unburned area and burned area. Eight soil subsamples were combined into each composite sample creating a total of four replicate samples per pair and eight per site. A 2.5-cm soil probe was used to collect mineral soil samples to a depth of 10 cm at sites. A small garden trowel was used to remove samples to a depth of 10 cm at five (Cinderella Mountain, Ward Mountain, and all Lick Creek Sites) of the 11 sites (because the high proportion of coarse fragments made collecting cores with a standard soil probe difficult. All samples were returned immediately to the laboratory or placed in a cooler for transport if travel times were greater than 1 h.

### Laboratory analyses

Samples of N-fixing and non-N-fixing plants were returned to the laboratory and placed in a convection oven at 60°C for 48 h. Once dry, the samples of each species were ground to 20 mesh by using a Wiley mill. These samples were sent to Woods Hole National Laboratory and analyzed for atom percent $^{15}N$.

Visible root matter was removed from soil samples by hand. Gravimetric moisture content was determined with approximately 10 g of soil (Gardner 1986). Fresh 25-g (oven-dried equivalent) subsamples of soil were extracted in 50 mL of 2 M KCl, filtered through Whatman No. 2 filter paper and analyzed colorimetrically for $NH_4^+$-N using the Berthelot reaction (Willis et al. 1993) and $NO_3^-$-N by nitration of salycilate (Yang et al. 1998). Potentially mineralizable N (PMN) was determined by a 14-day anaerobic incubation (Hart et al. 1994). Fresh 5-g (oven-dry equivalent) subsamples were placed in centrifuge tubes, covered with 12.5 mL of water, the head space air was displaced with $N_2$, and the tubes were sealed and incubated for 14 days at 25°C. Ammonium was then extracted from the soil samples by adding 12.5 mL of 4 M KCl to each tube, shaking for 30 min, and filtering through Whatman No. 2 filter papers. The extracts were then analyzed for $NH_4^+$-N as described above.

Air-dry soil was sieved through a 2-mm sieve. Soil pH was determined in 0.01 M $CaCl_2$ (2:1 solution:soil) by using an Orion 701A pH meter. Dried soil samples were analyzed for water holding capacity at –30 kPa (Cassel and Nielsen 1986), and particle size distribution, by hydrometer (Gee and Bauder 1986). Soils were also ground to pass a 200-mesh sieve and analyzed for total C and N by dry combustion using a Fissions EA 1100 elemental analyzer (Fissions Instruments, Milano, Italy).

### Statistical analyses

Past work has shown that vegetation survey data is often non-normally distributed (Towne and Knapp 1996; Mueller-Dombois and Ellenberg 1974), so cover and frequency proportions were tested for normality using Kolmogorov–Smirnov test. This test showed significant non-normality in the data so the non-parametric Mann–Whitney *U* test was used in comparisons of vegetation data. Cover and frequency of N-fixing plants in burned and unburned plots were compared at each site in which N-fixing plants were found. Occurrence and abundance of N-fixing plants in wildfire and underburned sites were compared in the same manner. Student's *t* tests were used to determine significant differences in PMN values between unburned and burn plots at each site. The PMN values, grouped by site type (undisturbed or repeatedly opened), were also analyzed with Student's *t* tests. Regression analyses were performed to test for the occurrence of a linear relationship between soil parameters and the abundance of N-fixing plants. All data were analyzed using SPSS.

## Results

Comparisons between unburned and burned sites and between undisturbed (those not harvested in last 50 years) and repeatedly opened sites were the focus of this study. Paired study pairs were chosen to preserve as much similarity as possible between treatments (Table 1). Factors like fire intensity and severity, elevation, and aspect varied between sites, and to analyze the effects of these differences, a much larger number of sites would have to be sampled.

Post-fire tree basal area did not differ significantly between burned and unburned plots (Table 2). Mean basal area varied somewhat across all sites, but basal area in the majority of sampled plots fell between 20 and 25 $m^2$/ha.

Soil textures were generally coarser in the Bitterroot National Forest sites, where soils formed predominantly from granitic till as parent material. Soils from Lolo National Forest sites formed from till or colluvium derived from heterogeneous metamorphic Belt Supergroup rocks and had finer textures but also higher percentages of coarse fragments (Table 3).

Occurrence of native N-fixing plants was inconsistent at most sites and percent coverage of these plants was generally low (Table 4). *Lupinus* was the most common genus

**Table 2.** Post-fire basal area ($m^2 \cdot ha^{-1}$) in sample plots for all 11 burned and unburned sites.

| Plot | Frenchtown | Cinderella Mountain | Squaw Peak | Alberton | Henry Peak | Echo Valley | Ward Mountain | Rock Creek | Lick Creek 1 | Lick Creek 2 | Lick Creek 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Unburned | 22 | 16 | 23 | 23 | 17 | 21 | 21 | 25 | 24 | 28 | 28 |
| Burn | 23 | 18 | 23 | 22 | 17 | 23 | 20 | 24 | 22 | 28 | 25 |

**Note:** There was no significant difference in basal areas between burned and unburned stands (*n* = 4).

**Table 3.** Selected physical and chemical properties of burned and unburned plots (*n* = 4).

| Site | Treatment | Sand (%) | Silt (%) | Clay (%) | pH | WHC (%)[a] | Total C (g/kg) | Total N (g/kg) | C/N |
|---|---|---|---|---|---|---|---|---|---|
| Frenchtown | Unburned | 23 | 53 | 24 | 5.7 | 31 | 12.8 | 0.85 | 15.06 |
| | Burn | 22 | 53 | 25 | 4.6[b] | 32 | 15.7 | 0.95 | 16.53 |
| Cinderella Mountain | Unburned | 46 | 33 | 21 | 5.8 | 18 | 27.8 | 1.3 | 21.38 |
| | Burn | 46 | 35 | 19 | 5.4[c] | 23 | 23.2 | 1.29 | 17.98 |
| Squaw Peak | Unburned | 33 | 57 | 11 | 5.5 | 25 | 15.9 | 0.92 | 17.28 |
| | Burn | 24 | 53 | 23 | 5.6 | 31 | 17.5 | 1.07 | 16.36 |
| Alberton | Unburned | 34 | 51 | 15 | 5.6 | 38 | 20.9 | 1.09 | 19.17 |
| | Burn | 35 | 47 | 17 | 5.9 | 31 | 24.4 | 1.5 | 16.27 |
| Henry Peak | Unburned | 39 | 45 | 16 | 5.9 | 42 | 25.5 | 1.29 | 19.77 |
| | Burn | 37 | 48 | 15 | 5.8 | 34 | 15 | 1.02 | 14.71 |
| Echo Valley | Unburned | 46 | 36 | 19 | 4.6 | 48 | 82.6 | 4.2 | 19.67 |
| | Burn | 51 | 33 | 16 | 4.8 | 47 | 56.7 | 3.39 | 16.73 |
| Ward Mountain | Unburned | 51 | 36 | 14 | 5.4 | 37 | 40.2 | 1.75 | 22.97 |
| | Burn | 48 | 38 | 14 | 6.1[d] | 26 | 21.9 | 1.35 | 16.22 |
| Rock Creek | Unburned | 64 | 27 | 9 | 5.3 | 17 | 21.7 | 0.97 | 22.37 |
| | Burn | 60 | 30 | 10 | 5.1 | 14 | 20.2 | 0.96 | 21.04 |
| Lick Creek 1 | Unburned | 59 | 29 | 12 | 5 | 20 | 20.9 | 1.03 | 20.29 |
| | Burn | 65 | 27 | 8 | 5.3 | 16 | 23.8 | 1.01 | 23.56 |
| Lick Creek 2 | Unburned | 53 | 37 | 10 | 4.9 | 28 | 22.6 | 1 | 22.60 |
| | Burn | 55 | 34 | 11 | 4.7 | 27 | 31.7 | 1.38 | 22.97 |
| Lick Creek 3 | Unburned | 63 | 29 | 9 | 5 | 18 | 17.4 | 0.85 | 20.47 |
| | Burn | 62 | 31 | 8 | 5.3 | 17 | 17.4 | 0.8 | 21.75 |

[a]WHC, water holding capacity, percent moisture at –30 kPa water potential.
[b]Significantly different from unburned control ($\alpha$ = 0.001).
[c]Significantly different from unburned control ($\alpha$ = 0.1).
[d]Significantly different from unburned control ($\alpha$ = 0.05).

encountered (Table 5), and it was represented by three different species (*L. laxiflorus*, *L. leucophyllus*, and *L. sericeus*). Nitrogen-fixing shrub species were much more scattered, often seen in small numbers near plot centers but only *Ceanothus velutinus* fell within shrub subplots at the Henry Peak site. There were no sites with multiple species of N-fixing plants found in sampled areas, but other species were sometimes seen in small numbers around the sampled subplots.

Nitrogen-fixing plants were found in sampled areas in 9 of 11 sites (Table 5), but only seven of the species typically found in western Montana (Jurgensen et al. 1979; Lackschewitz 1991) were represented. The numbers reported for each site are averages of all subplots from the three sets of plots on which vegetation surveys were conducted (*n* = 12). Averages of frequency values showed a similar pattern, but values were generally higher (Table 4).

Large numbers of plots without N-fixing plants resulted in skewed, non-normal distributions for both presence and abundance of N-fixing plants across sites. Efforts to normalize the data using various transformations were not successful, so nonparametric tests were used for statistical analysis. Proportion of cover occupied by N-fixing plants was significantly higher in burned compared with unburned stands ($P \leq 0.05$) when all sites were analyzed together; however, when sites were analyzed separately, only one site in the Lick Creek Demonstration Area showed a significantly higher proportion of cover ($P \leq 0.1$). Comparisons of grouped data are provided in Table 6. The proportion of cover of N-fixing species was significantly higher in the burned plots when repeatedly opened sites were analyzed separately ($P \leq 0.05$), while undisturbed sites showed no significant differences between burned and unburned stands. When management histories were compared, repeatedly opened sites showed higher cover proportions of N-fixing plants than undisturbed sites with data from both burned and unburned stands included ($P \leq 0.001$). Similarly, burned and repeatedly open sites showed significantly higher cover proportions than the undisturbed burned sites ($P \leq 0.001$). However, cover proportions in unburned stands were not significantly different between repeatedly opened and undisturbed sites.

Frequency of occurrence of N-fixing plants showed similar trends (Table 4). Burned plots had a higher frequency of occurrence than unburned plots ($P \leq 0.001$). Again, sites that had been opened repeatedly had significantly higher

**Table 4.** Mean cover proportion and frequency of occurrence of N-fixing shrubs and herbs at 9 of the 11 sites studied in western Montana.

| | Cover proportion | | Frequency | |
|---|---|---|---|---|
| Site | Unburned | Burn | Unburned | Burn |
| Frenchtown | 0.0000 | 0.0010 | 0.0000 | 0.0625 |
| Squaw Peak | 0.0140 | 0.0267 | 0.2083 | 0.3750 |
| Alberton | 0.0027 | 0.0042 | 0.0625 | 0.1042 |
| Henry Peak | 0.0058 | 0.0010 | 0.0069 | 0.0069 |
| Echo Valley | 0.0204 | 0.0325 | 0.3125 | 0.5208 |
| Rock Creek | 0.0004 | 0.0019 | 0.0208 | 0.0417 |
| Lick Creek 1 | 0.0000 | 0.0060 | 0.0000 | 0.1875 |
| Lick Creek 2 | 0.0033 | 0.0183 | 0.0833 | 0.2708 |
| Lick Creek 3 | 0.0663 | 0.11625[a] | 0.5417 | 0.875[b] |
| Mean | 0.0125 | 0.0231[b] | 0.1402 | 0.2731[b] |

**Note:** Cinderella Mountain and Ward Peak had no N-fixing species present within plot areas.
[a]Significantly different from unburned control ($\alpha = 0.1$).
[b]Significantly different from unburned control ($\alpha = 0.05$).

frequency of occurrence ($P \leq 0.05$), while undisturbed sites did not show a significant difference between unburned and burned plots. Repeatedly opened sites showed higher frequency of occurrence of N fixers than undisturbed sites when unburned and burned plots were included in the analysis ($P \leq 0.001$). When analyzed separately unburned plots were not significantly different between repeatedly opened sites and undisturbed sites, but burned plots in opened sites had higher frequencies of N-fixing plant occurrence than undisturbed sites ($P \leq 0.001$).

Nitrogen-fixing plants had lower $\delta^{15}N$ values than non-fixing plants for all of the samples except in the case of the non-N-fixing weed spotted knapweed (*Centaurea maculosa*). However, in a separate study we have found small but measurable rates of acetylene reduction on the surfaces of unwashed knapweed roots likely as a result of an associative free-living N fixing bacteria (T.H. DeLuca and R.A. Sheridan, unpublished data). Average $\delta^{15}N$ values for N-fixing plants were –0.55 compared with an average value of 1.04 for non-N-fixing plants (1.55 excluding knapweed), demonstrating active N fixation by the legumes found at the study sites in this project.

Soil water holding capacity (WHC) and percent sand, silt, and clay did not differ significantly between treatments at each site (Table 3). Soil pH varied somewhat between burned and unburned stands at three locations. Total C and N data along with C/N are also presented in Table 3, and overall, there were no significant differences in these values between burned and unburned stands. There was no evident correlation between cover proportion or frequency of occurrence of N-fixing plants and any of the soil physical or chemical properties in the 11 sites sampled for this study.

Potentially mineralizable N values tended to be greater in unburned than in burned plots and were significantly higher than PMN values for burned plots ($P \leq 0.01$) when all sites were analyzed together (Table 7). Sites repeatedly opened by harvest and those not disturbed for over 50 years were analyzed separately, and both groups showed significantly higher PMN values in unburned versus burned plots (Table 6). Unburned plots in repeatedly opened sites had somewhat greater PMN than burned plots ($P \leq 0.1$). The PMN values in unburned plots of undisturbed sites (those not harvested in the last 50 years) were significantly greater than in burned plots ($P \leq 0.05$). When the two types of sites were compared, undisturbed sites had significantly higher PMN values than those sites that were repeatedly opened with data from both unburned and burned plots included $P \leq 0.05$). Unburned and burned plots of undisturbed sites were significantly higher in PMN than their counterparts in repeatedly opened sites (unburned plots at $P \leq 0.05$ and burned at $P \leq 0.1$) (Table 5).

**Table 5.** Nitrogen-fixing species found in study sites, either within subplots, or near plot centers, but outside of the actual sampled areas.

| Species | In sample subplots | Near plot centers |
|---|---|---|
| *Ceanothus velutinus* | HP | R |
| *Lupinus argenteus* | | A |
| *L. laxiflorus* | EV | |
| *L. leucophyllus* | R, LC, LL, K | |
| *L. sericeus* | F, SP, A | |
| *Purshia tridentata* | | HP, LL |
| *Shepherdia canadensis* | | HP, R, LC |

**Note:** Abbreviations for site are as follows: F, Frenchtown; CM, Cinderella Mountain; SP, Squaw Peak; A, Alberton; HP, Henry Peak; EV, Echo Valley; W, Ward Mountain; R, Rock Creek; LC, Lick Creek 1; LL, Lick Creek 2; K, Lick Creek 3.

**Table 6.** Comparisons of PMN and N-fixing vegetative cover proportions between treatments and between sites with different management histories.

| | PMN (mg/kg) | | Cover proportion | |
|---|---|---|---|---|
| Comparison | Mean | *P* | Mean | *P* |
| Opened ($n$ = 10) | 11.51 | 0.004 | 0.026 | 0.001 |
| Undisturbed ($n$ = 12) | 18.03 | | 0.007 | |
| Unburned opened ($n$ = 5) | 13.85 | 0.016 | 0.018 | 0.200 |
| Unburned undisturbed ($n$ = 6) | 21.83 | | 0.006 | |
| Burn opened ($n$ = 5) | 9.17 | 0.089 | 0.035 | 0.001 |
| Burn undisturbed ($n$ = 6) | 14.23 | | 0.008 | |
| Unburned opened ($n$ = 5) | 13.85 | 0.085 | 0.018 | 0.010 |
| Burn opened ($n$ = 5) | 9.17 | | 0.035 | |
| Unburned undisturbed ($n$ = 6) | 21.83 | 0.033 | 0.006 | 0.613 |
| Burn undisturbed ($n$ = 6) | 14.23 | | 0.008 | |

Potentially mineralizable N, expressed as a fraction of total N (Table 7), was also significantly greater ($P \leq 0.05$) in the unburned compared with the burned stands when averaged across all sites. Only two sites also showed significantly different PMN to total N ratios when sites were examined individually.

Extractable nitrate concentrations were generally higher in unburned stands than in burned stands (Fig. 1) and significantly higher when averaged across sites ($P \leq 0.001$). Levels of extractable ammonium were not significantly different between unburned and burned stands when averaged across sites and was significantly higher ($P \leq 0.01$) in the unburned versus the burned stand only at Henry Peak.

There is no apparent correlation between PMN levels and proportion of cover or frequency of N-fixing plants, even

**Table 7.** Levels of potentially mineralizable N (PMN) and PMN to total N ratios for burned and unburned sites in western Montana ($n$ = 4).

| Site | PMN (mg/kg) | | PMN/total N (%) | |
|---|---|---|---|---|
| | Unburned | Burned | Unburned | Burned |
| Frenchtown | 10.981 | 10.540 | 1.29 | 1.11 |
| Cinderella Mountain | 11.685 | 4.726[a] | 0.90 | 0.37[a] |
| Squaw Peak | 14.727 | 12.652 | 1.60 | 1.18 |
| Alberton | 18.660 | 25.597 | 1.71 | 1.71 |
| Henry Peak | 30.539 | 11.394 | 2.37 | 1.15 |
| Echo Valley | 35.073 | 19.290[b] | 0.86 | 0.57 |
| Ward Mountain | 27.920 | 8.881[c] | 1.60 | 0.66[c] |
| Rock Creek | 5.372 | 5.302 | 0.55 | 0.55 |
| Lick Creek 1 | 12.889 | 7.204 | 1.25 | 0.71 |
| Lick Creek 2 | 14.745 | 14.747 | 1.47 | 1.07 |
| Lick Creek 3 | 8.562 | 5.341 | 1.01 | 0.69 |
| Mean ($n$ = 11) | 17.477 | 11.471[c] | 1.33 | 0.89[c] |

[a]Significantly different from unburned control ($\alpha$ = 0.001).
[b]Significantly different from unburned control ($\alpha$ = 0.1).
[c]Significantly different from unburned control ($\alpha$ = 0.05).

though inverse trends were seen in these data. Potentially mineralizable N values were significantly higher on unburned sites and in undisturbed sites, while cover and frequency of N-fixing plants were lower in unburned and undisturbed sites (Table 5). There does not appear to be a pattern relating PMN level and moisture content across all sites; however, PMN levels do seem to vary with moisture content at six sites from the LNF. There are no significant differences in moisture content between unburned and burned stands when averaged across all sites.

## Discussion

Surprisingly few species of N-fixing plants were identified in sampled areas of the study sites and in no sites were multiple N-fixing species found in sampled areas. Low light intensities and competition from young trees seem to be plausible reasons for the limited occurrence of N-fixing plants from second-growth forests. It is possible that, once N-fixing plants have been excluded from these systems for long periods, factors such as decreased seed bank, relatively high levels of available N, or loss of colonizing symbiotic bacteria may prevent the effective establishment of these plants.

In the current study, sites that had been opened repeatedly had greater cover and frequency of N-fixing plants, and recently burned plots from both types of sites also showed higher cover and frequency. This is in agreement with previous findings that have shown increased density of N-fixing plants after fire in forests in the United States (Boring et al. 1990; Johnson 1995). However, in contrast to these study sites where N-fixing plants were a significant, sometimes dominant, component of understory vegetation post-fire, our sites had very low total occurrence of N-fixing plants. Other researchers have documented high densities of *Ceanothus* spp. and *Purshia tridentata* in some western Montana forest sites after fire (Fischer and Bradley 1987). The current work was performed in second-growth stands, which characteristically have a more dense litter layer, a more dense overstory (of predominantly Douglas-fir), an increased soil organic matter accumulation, increased PMN,, and possibly lower seed bank and microbial diversity compared with old-growth ponderosa pine forests. All of these factors could lead to a decline in the activity of N-fixing plant species prior to the reintroduction of fire.

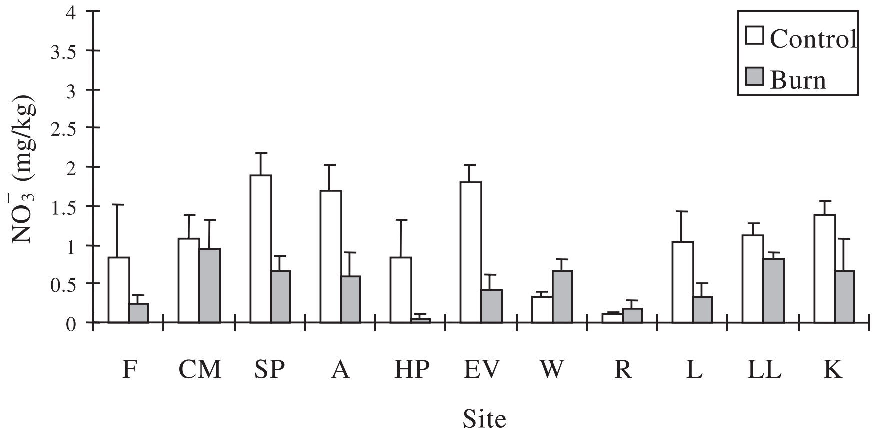
Research on Midwestern prairie ecosystems has demonstrated that long-term fire exclusion may lead to a decline in the number and diversity of viable seeds of native N-fixing plant species (Leach and Givnish 1996). These researchers also suggested that the increase in available N over time may have further suppressed recolonization by native N-fixing plant species. High levels of N are known to inhibit nodulation by *Rhizobium* and *Frankia* bacteria (Dawson 1993). In our studies, average levels of nitrate and PMN (indices of available N) were greatest in undisturbed stands. These stands also had the lowest occurrence of native N-fixing species. Lack of survival of inoculum prior to disturbance is another possible mechanism for failure of recolonization. Inoculum survival has been studied extensively in agricultural systems that have had artificial inoculum added to ensure nodulation (e.g., Klubeck et al. 1988).

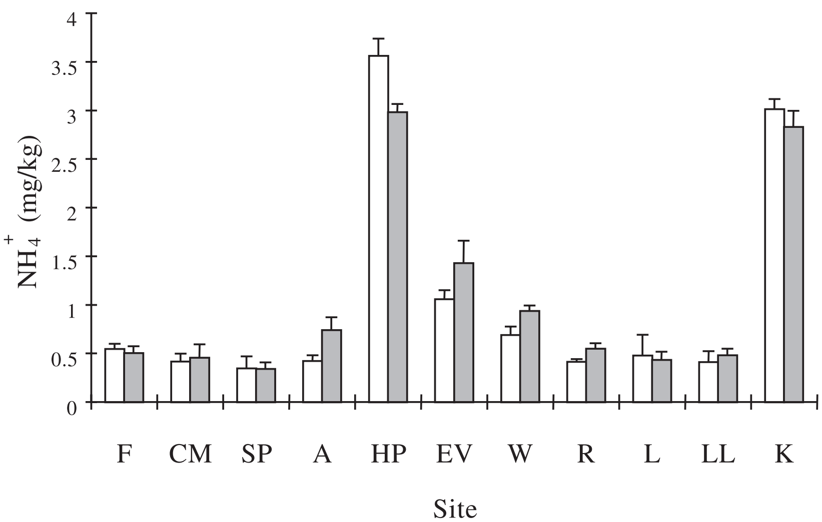
It is impossible to tell if fire exclusion has affected the total number of N-fixing species observed in western Montana forests the same as fire exclusion has reduced the presence and diversity of N-fixing plant species in prairie remnants (Leach and Givnish 1996). Over the past 100 years, large areas of forested land in the Inland Northwest have been exposed to other disturbances, from clear-cutting to intensive grazing, while fire has been excluded. Further research is required to examine native N-fixing plant species abundance and diversity in sites frequently affected by different disturbances, including fire, and sites where disturbances have been excluded.

Repeatedly opened sites and burned sites examined in this study showed lower PMN values along with higher cover and frequency of N-fixing plants. Nitrogen-fixing plants in prairie ecosystems have been seen in greater abundance in more N-limited lowlands than uplands and in fire-exposed sites compared with undisturbed sites (Towne and Knapp 1996). Colonization by legumes and actinorhizal plants in prairie ecosystems is favored by low soil N availability (Leach and Givnish 1996). Nitrogen-fixing plants also provide relatively easily decomposed, high N content (“high quality”) litter to soil (White et al. 1988; Hendricks and Boring 1992; Killingbeck 1996). Legumes and actinorhizal plants may have protected long-term site productivity by colonizing N-limited sites and increasing soil N levels.

Results showing decreased soil PMN levels in burned plots compared with unburned plots in this study are consistent with other work in the northwestern United States ponderosa pine forests (Monleon et al. 1997; DeLuca and Zouhar 2000). Lower levels of PMN in repeatedly opened sites compared with the less-disturbed sites, regardless of stand type, suggest that other types of disturbance and repeated disturbance also reduce PMN levels. Most researchers attribute lower levels of PMN in fire affected areas to loss of labile N to volatilization during fire and to reduced amounts of surface organic matter following fire (White 1986; Boring et al. 1990; Hungerford et al. 1991; Covington

**Fig. 1.** Nitrate and ammonium concentrations (mg/kg) for burned and unburned control sites ($n$ = 4) in western Montana. F, Frenchtown; CM, Cinderella Mountain; SP, Squaw Peak; A, Alberton; HP, Henry Peak; EV, Echo Valley; W, Ward Mountain; R, Rock Creek; LC, Lick Creek 1; LL, Lick Creek 2; K, Lick Creek 3.




and Sackett 1992; Kimmins 1996; DeLuca and Zouhar 1999; Neary et al. 1999). Perhaps this difference also led to reduced nitrate levels in burned plots. Frequent fire intervals may lead to long-term losses of surface and subsurface organic matter (Kimmins 1996; Jurgensen et al. 1997; Neary et al. 1999).

Reintroduction of fire into second-growth ponderosa pine – Douglas-fir stands has been shown to lower mineralizable N levels (Monleon et al. 1997; DeLuca and Zouhar 2000) and reduce stand productivity (Monleon et al. 1997). However, it is not clear how organic N accumulation in fire-excluded forests will influence site productivity. Composition and function of understory plants may play an important role in maintaining the quality of soil organic N resources and, therefore, the long-term productivity of pine stands. Sites with well-developed understory communities in ponderosa pine forests in central Oregon showed increased long-term growth of trees, total organic matter, and microbial biomass compared with sites in which understory vegetation had been excluded for 35 years (Busse et al. 1996). Two actinorhizal shrubs, *Ceanothus velutinus* and *Purshia tridentata*, were dominant plants in the understory community at this site and $^{15}N$ analysis was used to estimate that 45–70% of N in these plants was derived from fixation. Our results suggest that the N-fixing plants sampled for $^{15}N$ analysis were actively fixing N, and it is likely that N-fixation contributed a significant amount of N to the total N content of these plants.

Studies in ponderosa pine forests of California and central Oregon have shown increases in organic matter and mineral N content under N-fixing plants (Johnson 1995; Busse et al. 1996). It is possible that the greater percent cover (7–12%) of N-fixing plants at the Lick Creek 3 site may be contributing to observed N accretion at this site (Zouhar and DeLuca 2000).

This study suggests that ponderosa pine – Douglas-fir forests with high-frequency fires may have once had higher densities of N-fixing plants. Repeatedly opened sites in ponderosa pine – Douglas-fir forests are likely the best representation of historic forest structure in western Montana because of the paucity of remaining old growth stands (Arno 1996). It was in these sites that greater cover and frequency of N-fixing plants were seen. Although overall cover (1.8%) and frequency (3.3%) of N-fixing plants were low, some repeatedly opened sites had significant numbers of N-fixing plants in the understory, with average frequencies of up to

33% and average cover of 12%. Increased cover of N-fixing plants in recently burned repeatedly opened sites compared with recently burned undisturbed sites in this study may have specific management implications. Efforts to restore pre-settlement forest conditions in these forests may allow managers to increase the density of N-fixing plants while meeting other management objectives. More information is required about the contribution of the plants seen in this study to the N cycle of western Montana forests. If N-fixing plants become more common with increased fire disturbance and available soil N continues to decline, input of N from N-fixing plants may become very important in maintaining forest productivity. Additionally, the absence of N-fixing species from the understory community may have a long-term impact on the quality of the soil organic matter (e.g., Jurgensen et al. 1997; Neary et al. 1999). Nitrogen-fixing plant species would not only increase the N accretion at a site, they would also provide the forest floor and mineral soil with a higher quality (low C/N and a low lignin/N) substrate compared with that of non-N-fixing woody shrubs or overstory pine and fir needles.

## Conclusions

Exclusion of fire from Inland Northwest forests has caused changes in forest structure, composition, and function. The results of this study indicate that abundance of important understory plants may have also been affected by past fire-suppression policies. Significant increases in cover and frequency of native N-fixing plants were seen in burned compared with unburned sites and also in repeatedly opened sites compared with undisturbed sites. Lower levels of PMN and ratios of PMN to total N were seen in the same types of sites that had higher N-fixing plant occurrence and abundance. The increased abundance of N-fixing plants in more-disturbed areas with lower available N followed predicted distribution patterns based on past work and the ecology of N-fixing plants. Legumes and actinorhizal plants were found in low densities in most sites, likely limiting their contribution to N availability. Increased cover and frequency of N-fixing plants in repeatedly opened sites, however, suggest that pre-settlement forests may have had higher densities of N-fixing plants.

Lower PMN levels and decreased ratios of PMN to total N may result from changes in quality of soil organic matter in burned and repeatedly opened sites. This does not correspond to evidence of higher productivity in the frequently burned historic pine stands. Past research has shown that the presence of N-fixing plants results in improved soil organic matter status and increased N availability in otherwise N-limited sites. Therefore, N-fixing plants may have once played an important role in maintaining site productivity in fire-dominated western Montana forests, but now appear to exist in a state of limited number and diversity that is not readily overcome by a single exposure to wildfire or prescribed fire.

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